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THE HYBRID ORIGIN OF *ELEOCHARIS MACOUNII*

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ABSTRACT

For nearly a century since its description, *Eleocharis macounii* Fernald has been known with certainty only from the type station in Québec. It has been treated as a synonym of either *Eleocharis intermedia* Schultes, *E. obtusa* (Willd.) Schultes, *E. ovata* (Roth) R. & S. or *E. palustris* (L.) R. & S., or as a hybrid. Various quantitative and qualitative morphological features suggest that it is a hybrid involving *E. intermedia* in series *Palustriformes* and *E. obtusa* in series *Ovatae*. *Eleocharis* × *macounii* is best distinguished from sympatric species by its rhizome internodes less than 2 mm long, presence of many culms of varying lengths arising from a single tuft and pale greenish-brown achenes with prominent keels and a rough cellular surface. This natural hybrid is of particular interest since it is the first reported in the genus *Eleocharis* in North America, and it involves different species groups within the genus.

Key Words: *Eleocharis* × *macounii*, Cyperaceae, hybrid, Québec, North America

INTRODUCTION

The genus *Eleocharis* (Cyperaceae), commonly known as the spikerushes, is receiving increasing attention in North America because of the potential use of several species in aquatic weed management in irrigation systems and in pollution abatement (e.g., Sutton, 1984). The classification and identification of many of the species remain problematic. One of the problems is the status of *Eleocharis macounii* Fernald, a plant described in 1899 from specimens collected by J. Macoun at North Wakefield, Québec.

Marie-Victorin (1935) treated *Eleocharis* × *macounii* as a species, noting that it was known only from the Gatineau River. Svenson (1937) also treated it as a species but suggested that it

was problematic, close to *E. intermedia* Schultes, and also had characteristics of the European *E. multicaulis* (Sm.) Desv. It was treated as a species in the 7th and 8th editions of Gray's Manual (Robinson and Fernald, 1908; Fernald, 1950). Fernald noted that *E. macounii* was similar to the North American *E. intermedia* Schultes and the European *E. carniolica* Koch. Later Svenson (1953) noted that *E. macounii* was best treated as "an estuarine modification of *E. obtusa* (Willd.) Schultes, and he treated it as a synonym of *E. obtusa* in his (1957) monograph suggesting that it was "a variant with elongated style base somewhere between *E. obtusa* and *E. ovata* (Roth) R. & S., in which some of the achenes are slightly trigonous." Svenson (*in* Kartesz and Kartesz, 1980) placed *E. macounii* in synonymy with *E. obtusa* var. *obtusa*. However, Hines (1975) in his monograph of the *E. ovata* complex (which includes *E. obtusa*) did not mention *E. macounii* under either *E. obtusa* or *E. ovata*.

Gleason and Cronquist (1965) placed *Eleocharis macounii* in synonymy with *E. intermedia*, and it is treated in the same way in the United States national list of scientific plant names (Anon., 1982).

With respect to Canadian literature, *Eleocharis macounii* was treated as a questionable synonym of *E. intermedia* by Scoggan (1978), omitted by Boivin (1967), and is not mentioned in the listing of the rare plants of Québec (Bouchard et al., 1983). In his recently published Cyperaceae of eastern Canada, Boivin (1992) placed *E. macounii* in synonymy with *E. ovata sensu lato* (i.e., including *E. obtusa*).

The only annotation on the type at GH is that of Boivin (dated 1979) which indicates his view that the material is referable to *E. palustris* (L.) R. & S. *sensu lato*, but with the rhizomes, a distinctive feature of the latter species, broken off. On the isotype sheet at CAN, S. G. Hay noted in 1988 that *E. macounii* is probably a partly sterile hybrid between *E. intermedia* and *E. obtusa* var. *jejuna* Fernald. Hay also uncovered another specimen of *E. macounii*, misidentified as *E. intermedia*, collected from Cascades (Malte 7.8.1913, CAN), a locality situated close to the type station.

In summation *Eleocharis macounii* has been regarded as a species, as part of the variation within one of four other taxa, or as a hybrid. The purpose of the present paper is to examine critically each of these possibilities, and particularly to consider the hypothesis that *E. macounii* is of hybrid origin.

METHODS

The percentage of fruit development was determined on 15 mature spikes from the type material of *Eleocharis macounii* at GH and CAN. Pollen from five different spikes, also from the type material, was stained using the phloxine and fast green technique (Owczarzak, 1952) to assess fertility.

In order to determine whether *E. macounii* was intermediate in quantitative characters, 10 characters (Table 1) were measured in thirty specimens of each of *E. intermedia*, *E. obtusa* and *E. ovata*. These were selected to represent variation over a broad area of eastern Canada. For *E. macounii* two culms from the right hand group of tufts and two from the left hand group on the holotype were measured. Sheath length (mm) was measured from the base of the culm to the top of the sheath. Sheath width was measured across the mouth. Culm width was measured 1 cm below the inflorescence. Culm height is the distance from the tip of the spike to the base of the culm. Scales (also frequently referred to as bracts) measured were in all cases taken from the middle of the inflorescence. The length of the scarious margin of the scale was measured from the apical margin back to where it was no longer translucent. The length of the achene was measured from the base of the basal portion below the bristles to the base of the tubercle.

Tubercle width was used to separate *E. ovata* and *E. obtusa* since it is more easily determined than stamen number and separates the species readily (Hines, 1975). Here plants with a tubercle less than .5 mm wide are treated as *E. ovata*, while plants with a tubercle more than .51 mm wide are treated as *E. obtusa*.

RESULTS AND DISCUSSION

Fernald (1899) noted with his original description of *Eleocharis macounii* that it resembled the European *E. carniolica* Koch in habit and inflorescence. He correctly noted, however, that *E. macounii* has a much broader tubercle (Figure 1B) than *E. carniolica*. Furthermore the surface of the achene of *E. carniolica* is not clearly cellular, but rather obscurely wrinkled longitudinally and the tubercle of *E. carniolica* has a much more distinct neck.

The European *Eleocharis multicaulis* (Sm.) Desv. is similar to *E. macounii* in some respects, but is a much more robust plant

Table 1. Minimum, maximum and mean values for 14 characters in four northeastern North American *Eleocharis* taxa. For *E. intermedia*, *E. obtusa* and *E. ovata*, $n = 30$. For *E. × macounii* $n = 4$, but see also accompanying description based on all available material. All measurements are in mm.

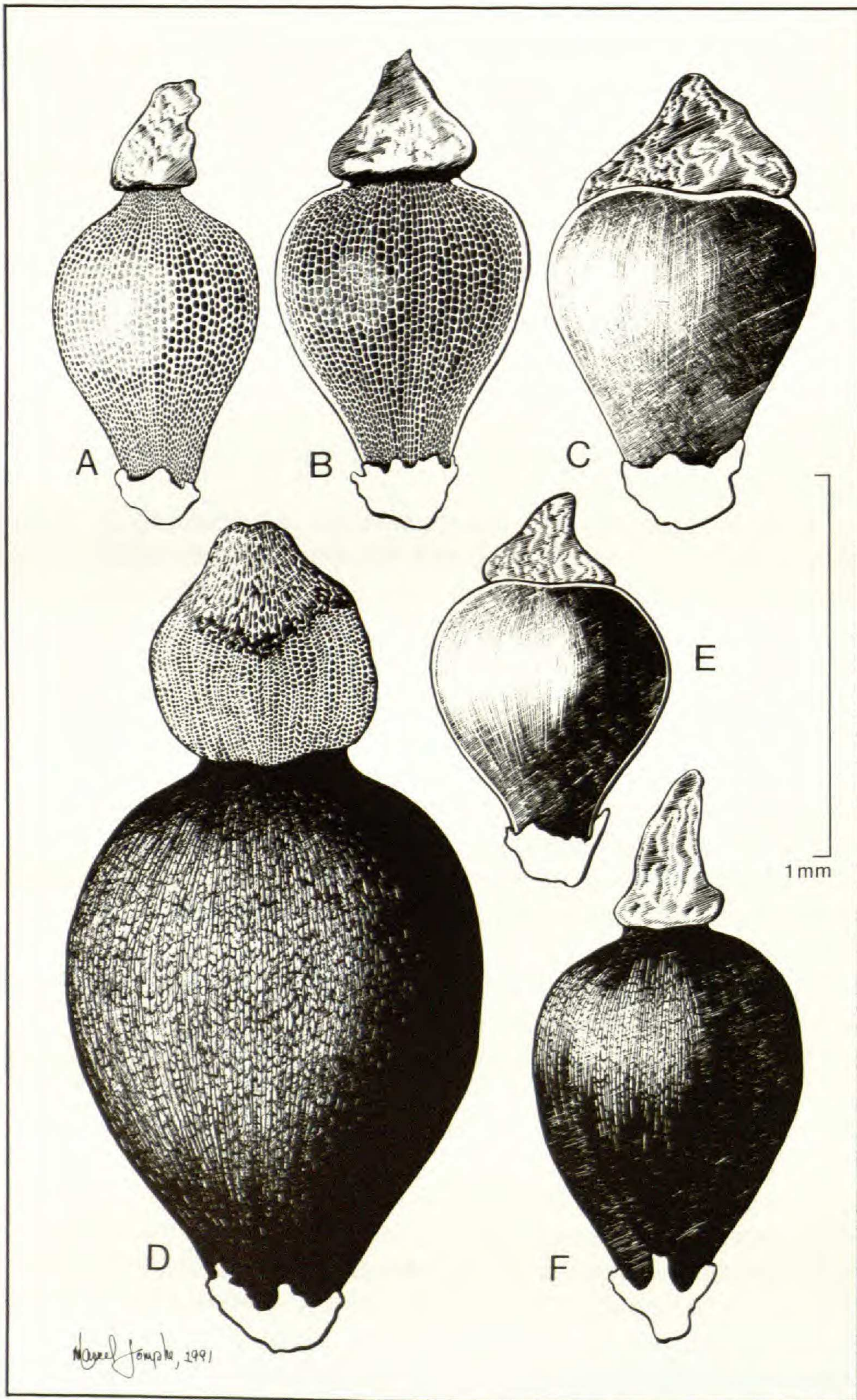
Character	<i>E. intermedia</i>			<i>E. ovata</i>			<i>E. obtusa</i>			<i>E. × macounii</i>		
	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
Sheath length	7.00	20.00	13.80	14.00	37.00	22.13	21.00	60.00	34.53	18.00	27.00	21.75
Sheath width	0.42	0.78	0.53	0.58	1.16	0.84	0.78	1.56	1.10	0.64	0.88	0.73
Culm width	0.30	0.40	0.34	0.36	0.82	0.56	0.56	1.24	0.77	0.50	0.74	0.58
Culm height	50.00	187.00	120.00	49.00	286.00	159.47	132.00	455.00	220.00	95.00	168.00	139.25
Spike length	3.90	7.00	5.05	4.00	9.00	5.81	4.50	11.50	7.26	8.50	11.50	10.15
Spike width	1.90	2.80	2.30	2.60	4.00	3.27	2.90	4.00	3.53	2.40	2.80	2.55
Scale length	1.70	2.10	1.91	1.70	2.20	1.89	1.74	2.30	1.96	2.26	2.36	2.30
Scale width	0.94	1.28	1.09	0.90	1.20	1.03	1.00	1.40	1.15	1.08	1.28	1.14
Scale width 0.2 mm from apex	0.16	0.40	0.22	0.40	0.70	0.54	0.46	0.72	0.61	0.48	0.68	0.57
Scale scarious apical margin width	0.02	0.12	0.07	0.10	0.24	0.18	0.12	0.24	0.20	0.16	0.18	0.17
Achene length	0.98	1.12	1.03	0.80	0.96	0.86	0.90	1.04	0.99	1.00	1.10	1.05
Achene width	0.60	0.70	0.64	0.60	0.76	0.68	0.70	0.86	0.79	0.68	0.76	0.72
Tubercle height	0.26	0.44	0.35	0.26	0.38	0.31	0.26	0.42	0.33	0.40	0.42	0.41
Tubercle width	0.18	0.22	0.20	0.32	0.44	0.37	0.54	0.74	0.63	0.38	0.43	0.41

with much longer scales and broader spikes. It also has a slightly longitudinally wrinkled achene surface unlike *E. macounii*. Thus *E. macounii* is not a European introduction.

Boivin suggested on his annotation label that the type material of *Eleocharis macounii* is referable to *E. palustris* with rhizomes broken off. This suggestion has to be rejected for several reasons: the cellular achene surface (Figure 1B), the presence of culms of varying lengths from very short to very long (Figure 2A), the fact of many culms arising from the same point on an abbreviated rhizome (Figure 2A), the elliptic scales (Figure 2C), the relatively broad tubercle (Figure 1B) and the relatively pale greenish-brown mature fruit are all characters lacking in *E. palustris sensu lato* (Figures 1D, F, 2E, H), including *E. erythropoda* Steudel (*E. calva*, and *E. smallii* Britton).

The type material of *E. macounii* does not represent a freak, because the plants do not show any abnormal growth or infection. Only 10–30% of the flowers on spikes of *E. macounii* have well developed fruit, the remainder being aborted. Many *Eleocharis* species including *E. intermedia*, *E. ovata*, and *E. obtusa* invariably have 95–100% of the flowers ripening into achenes, in the absence of obvious fungus infection or insect attack. The high level of fruit abortion in *E. macounii* suggests that it may be a hybrid. The hybrid concept is further supported by pollen infertility since only 10% of the pollen from one spike and 40% of the pollen from another spike, both from the holotype of *E. macounii*, took up the stain. In contrast more than 90% of pollen grains from *E. intermedia*, *E. ovata*, and *E. obtusa* stained well. Even in the *E. macounii* pollen that did stain, the stain was often pale or confined to a small part of the grain.

The cellular, three-sided and greenish surface of the achenes on the holotype plants of *Eleocharis macounii* (Figure 1B) is suggestive of *E. intermedia* (Figure 1A), although these characters are less pronounced than in the latter species. If *E. intermedia* is one parent, as evidenced by the cellular achene surface, then the other parent may be expected to possess certain features expressed in *E. macounii*, but not in *E. intermedia*. Among these characters that are to be expected is a broad tubercle (Figure 1B), a keeled and lenticular achene, a relatively long spike, and blunt, broad-tipped scales that have a relatively broad hyaline margin apically. There are two possibilities in the general region: *E. obtusa* (Figures 1C, 2D) and *E. ovata* (Figures 1E, 2G). *Eleocharis erythropoda*



(previously widely known as *E. calva*) and the *E. smallii-palustris* complex are eliminated as a source of putative parents because a hybrid of either of them with *E. intermedia* would be expected to have more pointed and broad-based scales and an achene with an elongate and fleshy tubercle and lacking prominently keeled edges, and rhizomes developed to a greater or lesser extent. *Eleocharis macounii* on the other hand has broadly rounded scales (Figure 2C), achenes with a relatively short tubercle and two or three prominently keeled edges (Figure 1B), and lacks an elongated rhizome. *Eleocharis obtusa* and *E. ovata*, however, both possess many of the characters to be expected in the other parent, notably the prominent keels on the achene, especially just below the tubercle. Both *E. obtusa* and *E. ovata* possessed values for various quantitative characters, such as tubercle width (Figure 1B) that were similar to *E. macounii* or intermediate with respect to *E. intermedia*. With regard to these two species, *E. ovata* has relatively short spikes and scales, and smaller achenes (Table 1), whereas relatively longer spikes and scales and larger achenes are predicted in the other parent if *E. macounii* were to be intermediate in these characters (Table 1). Since intermediacy is likely in many features of hybrids, *E. obtusa* is a more likely parent. It seems undesirable to recognize the var. *jejuna* of the latter species (e.g., Hines, 1975). The local rarity of *E. ovata* (Di Labio and Brunton, 1989; see also *M. O. Malte*, 4 Sept. 1922, sub *E. intermedia*, CAN) and the fact that it has not been found at Wakefield, where *E. obtusa* is common, also suggests that the latter is more likely to be the other parent.

Eleocharis × *macounii* appears to be the first hybrid reported in the genus *Eleocharis* in North America, and it should at least raise the question of whether hybridization is more widespread in the genus than currently recognized, and associated with some of the taxonomic difficulties.

Natural hybrids in *Eleocharis* have been reported from Japan (e.g., Koyama, 1961), and hybrids in *Eleocharis* subseries *Palustres* in Europe have been well documented (Strandhede, 1965)

←
Figure 1. Representative fruits of A *Eleocharis intermedia* (Catling 7/09/87, DAO). B *E. × macounii* (Macoun 7552, GH). C *E. obtusa* (Cody 6579, DAO). D *E. palustris* (Gillet 11765, DAO). E *E. ovata* (Dore 24360, DAO). F *E. erythropoda* (Rolland-Germain 10284, DAO). Drawings by Marcel Jomphe.

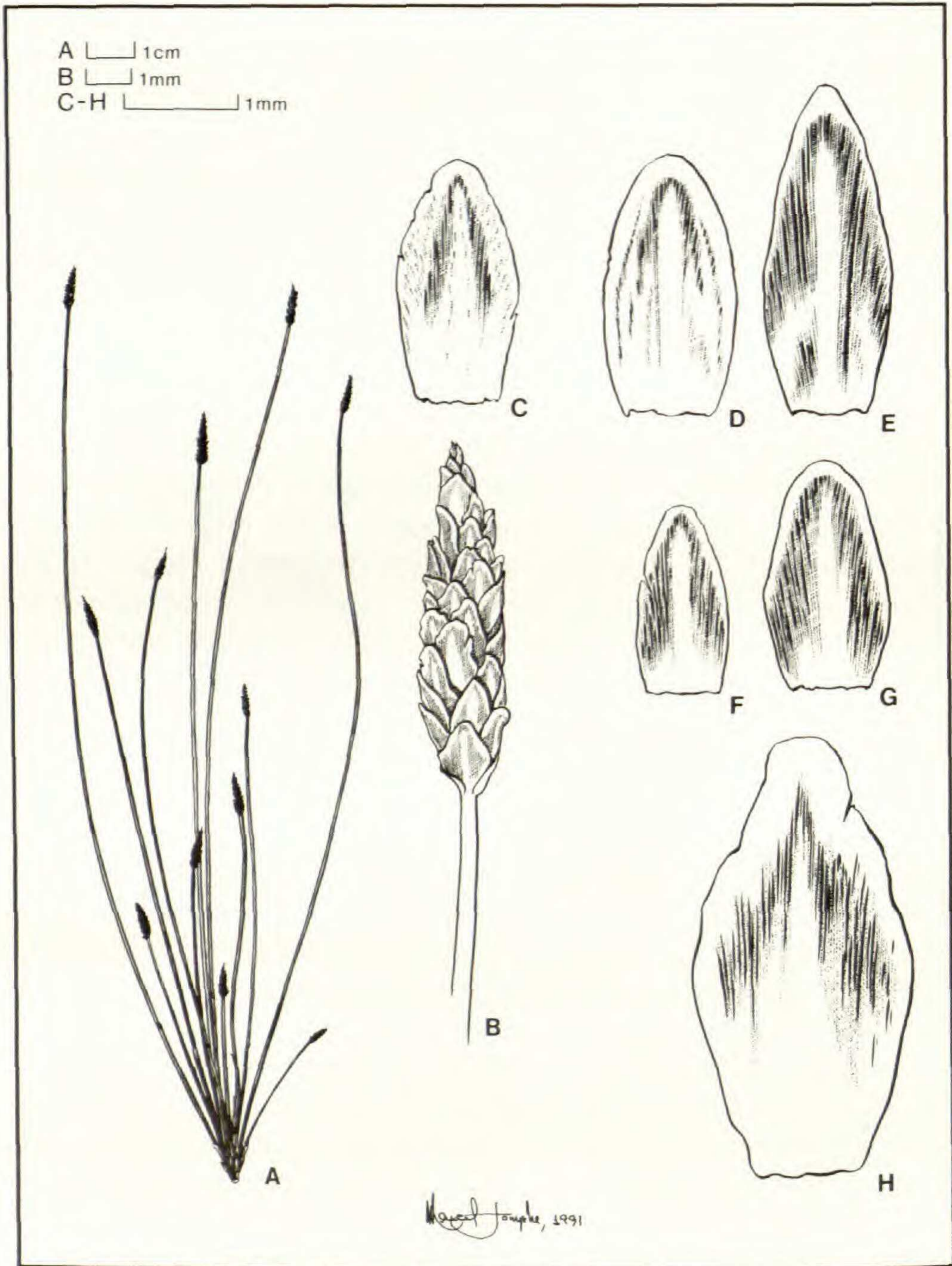


Figure 2. A-C *Eleocharis* × *macounii* (Macoun 7552, GH). A habit. B spikelet. C lower inflorescence scale. D-H lower inflorescence scales of various *Eleocharis* species. D *E. obtusa* (Cody 6759, DAO). E *E. erythropoda* (Rolland-Germain 10284, DAO). F *E. intermedia* (Catling 7/09/87, DAO). G *E. ovata* (Dore 24360, DAO). H *E. smallii* (sub *E. palustris* var. *major*, Gillet 11765, DAO). Drawings by Marcel Jomphe.

with cytological studies. *Eleocharis mamillata* subsp. *mamillata* × *E. palustris* subsp. *palustris* has greatly reduced fertility. It is to be expected that a hybrid between quite different species in different series (as treated by Svenson, 1957), like *E.* × *macounii*, would also have reduced fertility. The chromosome number of *E. obtusa* is $2n=10$, whereas *E. intermedia* has been reported with $2n=22$ (Schuyler, 1977), so that if living plants of *E.* × *macounii* are discovered, it should be possible to support the putative parentage with both chromosome number and meiotic anomalies. Unfortunately repeated attempts by the authors and other botanists to locate living material of *E.* × *macounii* at the type station and elsewhere have been unsuccessful.

The following key and description, based on the type material and one other collection, will facilitate the identification of *E.* × *macounii*.

KEY TO THE *ELEOCHARIS* SPECIES OF
SOUTHERN ONTARIO AND QUÉBEC WITH
DIFFERENTIATED TUBERCLES, FIRM SHEATHS AND
ACHENES LACKING LONGITUDINAL RIDGES

1. Rhizome internodes more than 2 mm long, tufts with most culms of similar height 2
 2. Achenes with a roughened cellular or reticulate surface, 3-sided
 - .. perennials of series *Palustriformes* subseries *Truncatae* including *E. compressa*, *E. elliptica* and *E. nitida*
 2. Achenes essentially smooth and shiny, at most only obscurely cellular or reticulate, 2-sided
 - .. perennials of series *Palustriformes* subseries *Palustris* including *E. erythropoda* and *E. smallii*
1. Rhizome internodes less than 2 mm long, tufts with culms of many different ages and heights 3
 3. Achenes with a roughened cellular or reticulate surface 4
 4. Longer spikelets 5–7 mm long; achenes becoming dark green, without prominent keels, subterete to equilateral triangular in cross section; tubercles 0.18–0.22 mm wide *E. intermedia*
 4. Longer spikelets 8–11 mm long; achenes pale greenish-brown, with 2 or 3 keels very prominent below tu-

- bercle, more or less lenticular in cross section; tubercles (0.2)0.3–0.5 mm wide *E. × macounii*
3. Achenes with a smooth surface 5
5. Tubercle less than 0.5 mm wide *E. ovata*
5. Tubercle 0.51 mm or more wide *E. obtusa*

Eleocharis × macounii Fernald (*pro sp.*) (*E. intermedia* Schultes × *E. obtusa* (Willd.) Schultes), Proc. Amer. Acad. 34: 497, Figure 26a. 1899.

TYPE: Québec, North Wakefield, 13 Sept. 1893, *J. Macoun* 75.5.2 (HOLOTYPE—GH! ISOTYPE—CAN!).

Annual herb; rhizome internodes less than 2 mm long, culms red at the base, green above, erect to divergent or bending downward, numerous, 20–230 mm long and of greatly varying lengths within a tuft, 0.3–0.8 mm wide 1 cm below the inflorescence; uppermost sheaths 5–35 mm long, 0.3–0.9 mm wide at the acute apex. Spikelets lanceolate, acute, densely 5–52-flowered, 3–11 mm long, 1.5–3 mm wide; scales reddish-brown with green midrib, ovate, obtuse, those in the middle of the spikelet 1.8–2.5 mm long, 1–1.3 mm wide, with a scarious margin 0.1–0.2 mm wide at the apex. Stamens 3, filaments 0.9–2 mm long, anthers 0.2–0.4 mm long, not reaching to the top of and concealed by the subtending scale, pollen largely infertile. Styles mostly trifid, occasionally bifid, the branches 0.5–0.9 mm long, extending beyond the tip of the subtending scale. Achenes mostly aborted, those maturing pale greenish-brown when fully mature, obovoid, 0.9–1.1 mm long (excluding tubercle), 0.6–0.8 mm wide, with mostly 3 (sometimes 2) keels becoming very prominent toward the apex, the surface rough-cellular, i.e., with circular or rectangular depressions with elevated walls; tubercle deltoid 0.3–0.4 mm high, 0.2–0.5 mm wide; bristles (4)5–6(7), brown, retrose, barbed, mostly 1.2–2.1 mm long, much exceeding the achene and tubercle.

Additional material examined: Québec: Cascades, 7-8-1913, *M. O. Malte s.n.* (CAN).

Distribution: Collected only from Wakefield and Cascades, both localities along the Gatineau River of Québec.

Comments: *Eleocharis × macounii* lacks elongate rhizomes and has the tufted or caespitose growth habit of *E. obtusa* and *E. intermedia*, as well as flowering/fruitle culms of many lengths as in these species. This latter feature, as well as the more or less

diverging culms, readily distinguishes it from *E. erythropoda*, which it otherwise resembles.

There is reason to suspect that *Eleocharis* × *macounii* may have culms longer than 230 mm and more than 1 mm wide, with larger spikelets than noted above, based on broken culms on tufts on both the holotype and isotype sheets, but these tufts cannot be identified with certainty. The material collected by *Malte* more closely resembles *E. intermedia* by its shorter culms and achenes with narrower tubercles.

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